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Landscape composition drives the impacts of artificial light at night on insectivorous bats ${}^{\bigstar}$

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ABSTRACT

Among the most prevalent sources of biodiversity declines, Artificial Light At Night (ALAN) is an emerging threat to global biodiversity. Much knowledge has already been gained to reduce impacts. However, the spatial variation of ALAN effects on biodiversity in interaction with landscape composition remains little studied, though it is of the utmost importance to identify lightscapes most in need of action. Several studies have shown that, at local scale, tree cover can intensify positive or negative effects of ALAN on biodiversity, but none have - at landscape scale - studied a wider range of landscape compositions around lit sites. We hypothesized that the magnitude of ALAN effects will depend on landscape composition and species' tolerance to light. Taking the case of insectivorous bats because of their varying sensitivity to ALAN, we investigated the species-specific activity response to ALAN. Bat activity was recorded along a gradient of light radiance. We ensured a large variability in landscape composition around 253 sampling sites. Among the 13 bat taxa studied, radiance decreased the activity of two groups of the slow-flying gleaner guild (Myotis and Plecotus spp.) and one species of the aerialhawking guild (Pipistrellus pipistrellus), and increased the activity of two species of the aerial-hawking guild (Pipistrellus kuhlii and Pipistrellus pygmaeus). Among these five effects, the magnitude of four of them was driven by landscape composition. For five other species, ALAN effects were only detectable in particular landscape compositions, making the main effect of radiance undetectable without account for interactions with landscape. Specifically, effects were strongest in non-urban habitats, for both guilds. Results highlight the importance to prioritize ALAN reduction efforts in non-urban habitats, and how important is to account for landscape composition when studying ALAN effects on bats to avoid missing effects.

1. Introduction

The loss and fragmentation of habitats constitute two of the main threats to global biodiversity (Monastersky, 2014). Therefore, both amount of semi-natural habitats and their spatial organization in landscapes drives species' habitat use and movements at multiple spatial scales (Ancillotto et al., 2019; Benton et al., 2003; Rybicki and Hanski, 2013; Sahraoui et al., 2021). For example, farming intensification and urbanization processes are widely recognized as strong pressures negatively affecting biodiversity by decreasing the amount of favourable habitat in landscapes (Peng et al., 2020; Salinas-Ramos et al., 2021). Such drivers can act as additive or synergistic pressures on biodiversity (Brook et al., 2008). Thus, the magnitude of pressures that affect biodiversity can depend on the heterogeneity in landscape composition

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or landscape structure (e.g. Caryl et al., 2016; Tamburini et al., 2016).

Artificial Light At Night (ALAN) is also an emerging threat to global biodiversity (Koen et al., 2018; Falchi et al., 2016; Kyba et al., 2017). ALAN affects biological rhythms (Gaston et al., 2017), fitness (e.g. de Jong et al., 2015), species movements (e.g. Doren et al., 2017) and has cascade effects on ecosystems (Bennie et al., 2018; Knop et al., 2017). All these ALAN effects are particularly well-known for insectivorous bats (Boldogh et al., 2008; Mathews et al., 2015; Rydell et al., 2017), and ALAN is even proposed as one of the main global threats to bats (Voigt and Kingston, 2016).

Studies have shown that ALAN reduced bat movements through barrier effects, thus generating habitat fragmentation and loss (Hale et al., 2015). Such effects can ultimately decrease habitats connectivity for bats within landscape (Laforge et al., 2019), connectivity being a key driver of bat activity and populations' health status (Frey-Ehrenbold et al., 2013; Froidevaux et al., 2017). However, how ALAN effects vary across landscape composition, remains little studied. It was recently shown that increasing tree cover 100-500 m around streetlights intensified negative and positive responses of bats to light (Straka et al., 2019). These authors also showed that tree cover can mitigate negative impacts of streetlights on open space foraging bats. Two other studies drew similar conclusions: in case of low tree cover proportion, ALAN had a negative impact on bat activity, while effects tended to be positive under high proportions (Mathews et al., 2015; Pauwels et al., 2019). Thus, accounting for spatial variations of ALAN effects according to landscape composition is of high importance to build efficient conservation strategies aiming to limit landscape functionality losses concerning bats.

Two deeply linked pressures can drive bat responses when studying the spatial variation of ALAN effects on insectivorous bats: (i) a decrease in the amount of habitats through their degradation or urbanization, which in turn reduces food resource for bats (i.e. arthropods; Sánchez-Bayo and Wyckhuys, 2019), and (ii) the artificial light level with its behavioural-induced changes (e.g. increased perceived predation risk and flight speed; Jones and Rydell, 1994; Polak et al., 2011) and its 'vacuum cleaner' effect, which aggregates arthropod preys around light sources while decreasing their amount in unlit areas (Eisenbeis, 2006; Owens and Lewis, 2018). Thus, bats are potentially constrained by the cost-benefit ratio of foraging at a given place driven by both habitat suitability and artificial light levels. In addition, bats' response to light likely depends on their flight strategy: aerial-hawking species (i.e. from genera such as *Eptesicus, Nyctalus* and *Pipistrellus*) appear to be less locally affected by ALAN by being able to exploit insects under light sources, while slow-flying gleaner species (i.e. from genera such as *Myotis* and *Plecotus*) avoid streetlights, potentially due to perceived predation risk (Stone et al., 2015). In addition, one aerial-hawking species, *P. pipistrellus*, although described as less affected by light at local scales (Azam et al., 2015, 2018), was found as negatively affected at regional (Pauwels et al., 2019) and national (Azam et al., 2016) scales. We thus specifically expected the global activity (i.e. not differentiating foraging from commuting) of *P. pipistrellus* to decrease with increasing ALAN.

As a consequence, we hypothesized that global activity of slow-flying gleaner species should decrease with ALAN, and this more strongly in non-urban habitats (areas composed of any land-use types other than impervious surfaces - such as housing, industrial areas or roads -, i.e. farmlands, forests, hedgerows and wetlands). This could be caused by an additive effect between (i) light sources repulsive effects (e.g. related to their intrinsic perception of increased predation risk; Jones and Rydell, 1994), and (ii) an increasing prey density in non-urban habitats irrespective of light as insects complete their life cycle on vegetation or in water (Lagucki et al., 2017). Thus, given that all bat species are expected to be more abundant in areas with more preys, artificial light sources at such places would have stronger repulsive effects on light-shy species such as slow-flying gleaners compared to places less attractive for these species in terms of prey (Fig. 1a). In contrast, we expect that global activity of aerial-hawking bat species would be less affected or even positively affected by ALAN, and this more strongly when the amount of non-urban habitats increases, thanks to an additive effect between (i) their ability to exploit insects around light sources (Azam et al., 2018) and (ii) higher insect density in non-urban habitats (Fig. 1b).

Focusing on a study area with a diversified landscape composition (i. e. the amount of each land-use/habitat) along a wide ALAN gradient, we aimed to investigate (i) the species-specific response to ALAN at landscape scale using satellite-based radiance as an indicator of artificial lighting for 10 bat species and three bat species groups, and (ii) response variations according to landscape composition around sampling sites (i. e. a few hundred meters around sampling sites). To achieve this goal, we selected sample sites (i) within a gradient of radiance, (ii) while accounting for all possible landscape contexts from the combination of



Fig. 1. Schematic representation of the tested hypothesis showing the expected variation of artificial light effects on bat activity according to landscape composition for slow-flying gleaner (a; e.g. *Myotis* and *Plecotus* groups) and aerial-hawking (b; e.g. *Eptesicus*, *Nyctalus* and *Pipistrellus* species) bats. The direction of the grey arrows shows the expected ways of increasing bat activity in term of light-landscape combinations, and the grey arrows width shows expected the magnitude of changes.

three land-uses (forest, urban, wetland), and (iii) making sure that landuses were not correlated with each other or with the radiance.

2. Materials and methods

2.1. Study area

We carried out the study over a 33,468 ha area around a highly urbanized city in France: Valence (Fig. 2). This area exhibits a wide radiance gradient (i.e. a measure of ALAN defined as the radiant flux reflected or emitted by surfaces) from 0 to 94 nW/cm²*sr. Land-use types in the study area were largely agricultural (54%), urban (21%), and forest (21%), while wetlands cover only 4% (Fig. 2; see Environmental variables section for information source). Note the agriculture land-use in the study area: 86% annual crops (mainly cereals and market gardening), 7% perennial crops (orchard and vineyard) and 7% grass-lands, with an average of 20 m of hedgerows per hectare.

2.2. Sampling design

The study aimed to investigate the radiance effects on bat activity (i. e. not differentiating foraging from commuting) according to landscape composition. For that we sampled bat activity at 253 sampling sites covering a wide range of radiance (from 0 to 57 nW/cm²*sr used as an indicator of artificial lighting (Azam et al., 2016); Fig. S1, higher than 57 radiance values were too scarce in the study area to be included in the sampling design). Within this radiance range we sought to include a high variability in land-use variables (see Environmental variables section) while minimising correlations between radiance and land-use variables (Figs. S2 & S3; Table S1). Accordingly, we selected sampling sites following the Laforge et al. (2019) approach. We first divided the whole study area into 250×250 m quadrats, whose mean radiance, forest

areas proportion, urban areas proportion and distance from the center of quadrats to wetland were calculated. We used these four variables only to select sites, in order to limit the number of possible combinations while maximising variability in landscape contexts. We then categorized each of these variables into four values classes, maximising the inter-class variance and minimising the intra-class variance, using the Jenks Algorithm (Jenks, 1977). On the study area, 133 combinations of four classes (i.e. each derived from the radiance, forest proportion, urban proportions or distance to wetlands) were available (see Supporting information S1). Thus, each combination was composed of a given class of radiance, forest proportion, urban proportion and distance to wetland. We randomly selected three quadrats per combination whenever possible (i.e. 253 quadrats selected in total; see Supporting information S1 for details on this quadrat selection method). The selected quadrats central points were defined as the location of sampling sites, or it was slightly moved when inaccessible.

2.3. Bat monitoring

Recordings were carried out from the 3 May to July 3, 2017, during 27 nights in the seasonal peak of bat activity according to the French national bat monitoring program "Vigie- Chiro" (http://www.vigie nature.fr), under favourable weather conditions: no rain; <5 m/s wind speeds, and >12 °C temperatures. The average nighttime cloud cover varied from 17 to 70% (47% in average; see Table S2).

We sampled on average nine sites per night simultaneously, covering a wide range of radiances (Table S2), with at least 750 m between each of them. Bats were recorded throughout the entire night, from 30 min before sunset to 30 min after sunrise, and only once. Echolocation calls were recorded using one SM4BAT (Wildlife Acoustics Inc., Concord, MA, USA) recorder per site (Supporting Information S2 for details about standardized settings).



Fig. 2. Map of the study area in France and the 253 sampling sites, according to the main land-use (a) and radiance gradient (b).

Since it is impossible to determine the number of individual bats from their echolocation calls, we calculated an activity metric commonly used in Europe, hereafter named 'bat passes', calculated as the number of bat passes per night (Kerbiriou et al., 2019, 2018; Stahlschmidt and Brühl, 2012). A bat pass was defined as a single or greater echolocation call separated by at least a 2-s gap without calls, and a maximum duration of 15 s. We did not separated foraging from commuting bat passes. We then automatically identified bat passes to the most accurate taxonomic level possible, using the SonoChiro© software (Biotope, France).

To account for potential errors in automated identifications, we followed the Barré et al. (2019) approach proposing a cautious method to ensure results robustness against automated identification errors in acoustic surveys. The method allows, resorting to random manual checking of automated identifications (by combining measurements of energy peak, final frequency, call duration, bandwidth and time between calls, as discussed in Barataud (2015)), to model the error rate for each species or group, according to confidence scores provided by the software (Supporting Information S3, Table S3 and Fig. S4). This method allows presenting results based on a maximum error rate tolerance of 0.5 (MERT), above which data were discarded. This keeps the number of bat passes for all species and species groups great enough for analysis, while limiting false positives. Then results are confirmed on a more restrictive 0.2 MERT, in order to permit conclusive interpretation only when both MERT thresholds are consistent (Barré et al., 2019; see Supporting Information S3, Tables S3 & S4 and Fig. S4 for more details).

Two species groups (i.e. *Myotis* spp. and *Plecotus* spp.) were constructed, because species within these groups were difficult to distinguish from each other, based on their echolocation calls (Obrist, Boesch & Fluckiger, 2004). We also constructed a third species group, *Rhinolophus* spp., including *Rhinolophus ferrumequinum* and *R. hipposideros*, because of their very low abundances and occurrences (Table S4).

2.4. Environmental variables

Since the effects of environmental variables on bat activity can change according to the spatial scale considered and are very context-dependent and difficult to predict, we calculated their metrics regarding average, proportion or length at five different buffer sizes used in previous studies (200, 400, 600, 800 and 1000 m; Kalda et al., 2015; Lacoeuilhe et al., 2016), using the QGIS software.

For each sampling site and each buffer size, we first extracted the average radiance in buffers from VIIRS night-time lights. Then, to characterize landscape composition, we computed 11 land-use variables (either distances or length/proportion in buffers) varying across sites (Table S5), which are well-known good bat activity predictors: the proportion of, and distance to urban (e.g. Azam et al., 2016), forest (e.g. Boughey et al., 2011), farmland (e.g. Roeleke et al., 2016) and wetland areas (e.g. Amorim et al., 2018; De Conno et al., 2018); hedgerow length (e.g. Froidevaux et al., 2017; Lacoeuilhe et al., 2016), road (e.g. Berthinussen & Altringham, 2012) and wooded edges (Heim et al., 2017).

Radiance was extracted from VIIRS night-time lights, which is a yearly and cloud-free composite raster (2016) with a 450-m pixel size produced by the Earth Observation Group and NOAA National Centres for Environmental Information (NCEI) (https://ngdc.noaa.gov/eog/v iirs/download_dnb_composites.html). Environmental variables (2016) were provided by the National Institute of Geography in a vectorial shapefile with a 2.5-m spatial accuracy (from BD TOPO for data on forests, hedgerows and urban areas, from BD Carthage for wetland data, from BD ORTHO and Graphical Parcel Register for farmland data).

2.5. Statistical analyses

We examined the radiance effects on bat activity according to landuse variables around sampling sites (i.e. landscape composition). A summary of the statistical analysis steps presented below is shown in

Fig. S5. We ran Generalized Linear Mixed Models (GLMMs, R package lme4; Bates et al., 2015) for each species or species group separately, using the number of bat passes per site as response variable. We used a negative binomial error distribution to keep low overdispersion ratios in models (<1.50; Table S5; Zuur et al., 2009). For two rare taxa (Barbastella barbastellus, Rhinolophus spp.; Table S3), information relative to bat activity variation were too scarce, thus we used the presence-absence per site as response variable associated with a binomial error distribution. To build full models, we included the radiance and land-use variables as fixed effects. In order to assess the dependence on landscape composition of potential radiance effects on bat activity, we included all possible simple interactions between radiance and land-use variables. All variables used as fixed effects were scaled (i.e. by subtracting the mean and dividing by the standard deviation). To control for inter-night variation in bat activity (e.g. due to weather conditions) and according to our sampling design based on simultaneous recordings each night along a radiance-landscape gradient, we included the date as random effect in models.

For each variable included in the full models presented above, except where distances are concerned, we selected the best buffer size for each species. To do this, we ran one univariate model per variable per buffer size for each species, and selected the one with the smallest Akaïke Information Criteria (AIC). Thus, each full model can contain different optimal buffer sizes between variables (Tables S6 & S7). Full models were constructed by excluding any explanatory variable responsible for multicollinearity with a <2 variance inflation factor (VIF) value using the vif function (R package car; Fox and Weisberg, 2019; see Supporting information S4 and table S6 for full models composition). Thus, removing variables responsible for multicollinearity restrained the number of predictors (ranging from 8 to 17) in full models, depending on species (Table S6). We also assessed potential non-linear effects for all variables by visual inspection of plots from Generalized Additive Mixed Models (GAMM, R package mgcv; Wood, 2011). Seven quadratic relationships were observed for B. barbastellus, Miniopterus schreibersii, Myotis spp., Pipistrellus kuhlii, Pipistrellus nathusii and Plecotus spp. To account for these non-linear relationships, we added quadratic effects on these variables in full GLMMs (Table S6). We also checked for potential spatial autocorrelation in model residuals using the Moran. I function to test significance (R package spatial; Venables and Ripley, 2002). We found significant spatial autocorrelation for Eptesicus serotinus, Myotis spp., Nyctalus leisleri, Nyctalus noctula and P. pipistrellus. To the full models, we added a distance-weighted variable in addition to other explanatory variables, to account for spatial autocorrelation (Table S6; Bardos et al., 2015), using the autocov_dist function (R package spdep; Bivand and Wong, 2018).

Then, following a multi-model inference approach (Grueber et al., 2011), we generated - from the full model for each species and species groups - a set of candidate models containing all possible variable combinations ranked by corrected AIC (AICc). Using all models with a delta AICc <2 (and a delta AICc <6 for comparison; Grueber et al., 2011), we averaged regression coefficients for each fixed effect, using the model. avg function (R package MuMIn; Barton, 2015). Fixed effects were averaged only over models in which that fixed effect appeared (i.e. the so-called natural average method; Grueber et al., 2011). From the model averaging procedure, we were also able to extract the relative importance of each variable (estimated by summing the weights of models in which the variable appeared) and the percentage of explained variance by full and best models (i.e. r squared), using the rsquared function (R package piecewise SEM; Lefcheck, 2016). As it is not possible to run the rsquared function on averaged models, we computed it for best and full models in order to provide a global view of the goodness-of-fit.

All analyses were performed in the R software v.3.5.1 (R Core Team, 2020).

3. Results

3.1. Bat monitoring

At the 253 sampling sites, we recorded 79,661 bat passes in total, including 10 species and three species groups, where the most abundant species was *P. kuhlii*, representing 71% of passes and present in 100% of sites (Table S3). The least common species were *E. serotinus* (43 passes), *Rhinolophus* spp. (32 passes) and *B. barbastellus* (208 passes), which were recorded respectively in 9%, 13% and 5% of sites (Table S3).

3.2. Radiance effects on bat activity

The radiance variable had a significant effect on the activity of five species or species groups (Table 1), with high relative importance (Table S8), and these were selected in all top candidate models with a <2 AICc delta for nine species or species groups, and in a minimum of 50% of top candidate models for the four remaining ones. We detected significant decrease in activity of *Myotis* spp., *Plecotus* spp. and *P. pipistrellus* due to radiance (Table 1; Fig. 3). We also detected significant increase in activity of *P. kuhlii* and *P. pygmaeus* due to radiance (Table 1; Fig. 3).

3.3. Interaction between radiance and landscape composition

Depending on species, best models (i.e. with the lowest AICc) explained a percentage of variance ranging between 7% and 34%, except for those from *E. serotinus* and *N. noctula*, which explained very low variance (i.e. 1 and < 0.1%, respectively; Table S6).

We found a significant interaction effect between radiance and landuse variables for 8 species or species groups (Table 1). The results of these interactions as a whole show that the positive or negative effects of light on bats, depending on species, mainly occurred in non-urban habitats. Specifically, bat activity becomes increasingly higher under high radiances with the increasing proportion of farmland areas for P. pygmaeus, while for N. noctula activity it is higher under low radiances with low proportions of farmland; and higher under high radiances with high farmland proportions (Table 1; Fig. 4). We found a similar result concerning H. savii and P. nathusii, whose activity increased with increasing radiance only when proportion of forests became high (Table 1; Fig. 4). However, we found higher activity of N. leisleri under high radiances far from forests (Table 1; Fig. 4). We also found higher H. savii activity under high radiances far from wetlands, while M. Schreibersii was positively affected by radiance below 700 m from wetlands and negatively affected above (Table 1; Fig. 4). We found the opposed pattern for N. noctula and N. leisleri, whose activity became higher under high radiances along with the increasing proportion of wetlands, although sampled gradients were less extensive (Table 1; Fig. 4).

Concerning urban variables, we found an increasing *M. schreibersii* activity with increasing radiance, which mainly occurred in non-urban habitats (Table 1; Fig. 4). We found the same pattern for *Myotis* spp., for which the decrease in activity due to radiance became much higher with increasing distance to urban areas, as well as the increase in *P. kuhlii* activity due to radiance, which became increasingly higher with increasing distance to urban areas (Table 1; Fig. 4). For these three species or group, radiance was positively associated with the increasing proportion of, or the decreasing distance to urban areas (Fig. S6), even though this did not result in any collinearity issue.

Results were qualitatively very similar and little changes were found after we re-ran analyses at the 0.2 maximum error rate threshold (see Table S9). However, two new significances were found for *P. pipistrellus*. Specifically, we found an increasingly negative effect of radiance on *P. pipistrellus* activity, with an increasing length of hedgerows and a decreasing distance to wetlands (Table S9; Figs. 4 and 5). Finally, averaging candidate models in a delta AICc <6 instead of 2 did not change results (Table S10).

4. Discussion

We show that for 9 bat taxa out of the 13 tested, ALAN affects bat activity (i.e. not differentiating foraging from commuting) especially in non-urban habitats. We also show that, as expected, the responses depend on the species. For five species, the intensity of ALAN (i.e. apart from its interactions with landscape variables) increased the activity of P. kuhlii and P. pygmaeus and decreased the activity of Myotis spp., Plecotus spp. and P. pipistrellus, and these effects were significantly driven by landscape composition. More notably, for five species, the ALAN effects on activity were only significant in particular landscape compositions (H. savii, M. schreibersii, N. leisleri, N. noctula and P. nathusii), which make such effects undetectable without exploring ALAN-landscape composition interactions. Specifically, both positive or negative ALAN effects on bat activity occur much more often in non-urban habitats. All these results highlight (i) the need to prioritize ALAN reduction efforts in non-urban habitats, (ii) how important is to account for landscape composition when studying ALAN effects on bats to avoid missing effects, and (iii) the need to consider both ALAN and landscape composition when designing and implementing green infrastructures (i.e. strategically planned European network of natural and semi-natural areas) (European Commission, 2009).

4.1. Radiance effects on bat activity

Overall responses of bat species to radiance were consistent with the literature for slow-flying/gleaner species (i.e. Myotis and Plecotus species) widely known to be negatively impacted by artificial lighting (e.g. Azam et al., 2018; Lacœuilhe et al., 2014). Possible explanations could be the relative high sensitivity of the bat eye to the blue part of light spectrum (Müller et al., 2009), the increase in abundance of less light-shy species at the expense of slow-flying gleaner species (Arlettaz et al., 2000), or the increased predation risk due to their slow flight (Jones and Rydell, 1994). Positive effects of radiance detected for P. kuhlii and P. pygmaeus (i.e. the aerial-hawking species guild) were consistent with literature based on local measures of ALAN (i.e. a street lamp level, e.g. Azam et al., 2015), likely due to increased insect density close to lights (Rydell, 1992). However, our results were opposed to those found by Azam et al. (2016) carried out at national scale. The negative effect detected on P. pipistrellus was consistent with studies carried out at national (Azam et al., 2016) or agglomeration scales (Pauwels et al., 2019). However, positive effects on P. Pipistrellus species are also reported at street light scale (e.g. Azam et al., 2018). Such opposed pattern could be explained by the scale effect and light variable used: (i) studies carried out at local scale involved ground-based data measurements at very small scales (a few meters) and focus on street light contexts, highlighting likely attractiveness of streetlight lamp for insects and, in turn, a number of bats, while (ii) studies carried out on a large scale (countries or cities) have more chances to involve more sampling of unlit areas close to and far from lit ones, which allows for detecting insects depletion due to the "vacuum cleaner" effect in unlit areas close to lit ones (Eisenbeis, 2006; Owens and Lewis, 2018).

4.2. Interaction between radiance and landscape composition

First, we found that radiance effects on bat vary among landscape compositions in bat-friendly non-urban habitats (i.e. farmland – including non-negligible amount of perennial crops and grasslands in the study area–, forest, hedgerow and wetland). Radiance had higher effects on bat activity with increasing non-urban habitats (i.e. an increasing amount of, or proximity to, land-uses other than impervious surfaces, or a decreasing amount of or proximity to urban areas). These results are in accordance with a recent study conducted at agglomeration scale, which showed that dense tree cover amplified positive or negative effects of street light for *P. pipistrellus*, *P. pygmaeus* and *Myotis* spp. (Straka et al., 2019). Two other studies showed that high tree cover

Table 1

Averaged estimates, standard errors in parentheses and significance levels (***P < 0.001, **P < 0.05, P < 0.1) from the set of best candidate models with an AICc delta <2 for each species (Barbar: Barbastella barbastellus; Eptser: Eptesicus serotinus; Hypsuy: Hypsuyo savii; Minsch: Miniopterus schreibersii; Myosp: Myotis spp.; Nyclei: Nyctalus leisleri; Nycnoc: Nyctalus noctula; Pipkuh: Pipistrellus kuhlii; Pipnat: Pipistrellus nathusii; Pippi: Pipistrellus; Pipsy: Pipistrellus pygnaeus; Plesp: Plecotus spp.; Rhisp: Rhinolophus spp.). Estimates show the effect of radiance and other environmental variables on bat activity. Significant results involving the radiance variable are indicated in bold. Empty cells represent cases for which the variable was not selected in the set of best candidate models.

| Variables | Estimated parameters, standard errors and p-values of averaged candidate models with Δ AICc <2 | | | | | | | | | | | | |
|--|---|--------------------|---------------------|---------------------|----------------------|---------------------|--------------------|------------------------|--------------------|----------------------|---------------------|---------------------|---------------------|
| | Barbar | Eptser | Hypsav | Minsch | Myosp | Nyclei | Nycnoc | Pipkuh | Pipnat | Pippip | Pippyg | Plesp | Rhisp |
| Artificial light va | riable | | | | | | | | | | | | |
| Radiance | -1.079 (2.120) | -0.837 (0.485). | 0.015 (0.009). | 0.094 (0.072) | -0.019 (0.010)* | -0.003 (0.003) | -0.001 (0.009) | 0.69e-3 (0.30e-3)* | 0.018 (0.011). | -0.005 (0.001)*** | 0.007 (0.002)*** | -0.111 (0.035)** | -1.983 (1.291) |
| Proportion varial | oles | | | | | | | | | | | | |
| Farmland | / | / | / | / | / | 0.002 (0.003) | -0.004 (0.010) | / | / | / | 0.001 (0.002) | / | / |
| Forest | 3.253 (1.436)* | / | 0.043 (0.008)*** | / | / | 1 | 1 | / | 0.036 (0.012)** | / | 1 | / | / |
| Urban | / | / | / | -0.195 (0.074)** | / | / | / | / | / | / | / | / | / |
| Wetland | 2.984 (1.105)** | 0.287 (0.327) | 0.013 (0.007). | 0.029 (0.068) | -0.008 (0.014) | -0.002 (0.003) | 0.024 (0.008)** | -0.21e-3 (0.20e-3) | 0.018 (0.009). | -0.001 (0.001). | 0.002 (0.002) | / | -1.115 (0.932) |
| Radiance: Farmland | 1 | 1 | | / | 1 | 1 | 0.022 (0.010)* | / | 1 | 1 | 0.003 (0.002)* | / | 1 |
| Radiance: Forest | / | / | 0.023 (0.008)** | / | / | / | / | / | 0.026 (0.013)* | / | 1 | / | / |
| Radiance: Urban | / | / | / | -0.196 (0.071)** | / | / | / | / | / | / | / | / | / |
| Radiance: Wetland | / | 0.468 (0.283). | 0.008 (0.005). | / | -0.032 (0.023) | 0.010 (0.003)*** | 0.026 (0.011)* | / | -0.008 (0.010) | -0.001 (0.001) | / | / | / |
| Distance to eleme | ent variables | | | | | | | | | | | | |
| Forest | / | -0.390 (0.411) | -0.010 (0.008) | -0.052 (0.067) | -0.027 (0.009)** | 0.002 (0.004) | 0.007 (0.008) | / | 0.031 (0.010)** | -0.001 (0.001) | -0.002 (0.002) | -0.046 (0.04) | -3.223 (2.092) |
| Hedgerow | / | 1 | 1 | 1 | | -0.005 (0.004) | 1 | / | 1 | -0.001 (0.001) | 1 | -0.064 (0.036). | 0.835 |
| Urban | / | -0.190 (0.406) | -0.026 (0.009)** | / | -0.011 (0.010) | -0.003 (0.003) | 0.005 (0.008) | 0.34e-3 (0.30e-3) | -0.028 (0.014). | -0.001 (0.001) | / | / | / |
| Wetland | / | -0.491 (0.425) | 0.008 (0.006) | -0.048 (0.067) | / | / | 0.004 (0.007) | 0.39e-3 (0.20e-3). | | -0.003 (0.001)** | 0.003 (0.002). | 0.058 (0.031). | -1.247 (0.783) |
| Radiance: Forest | / | 1 | 1 | 1 | -0.013 (0.009) | 0.010 (0.004)** | 1 | / | 0.021 (0.011). | -0.002 (0.001). | -0.003 (0.002) | / | -3.073 (1.807). |
| Radiance: Hedgerow | / | / | / | / | 1 | -0.007 (0.004) | / | / | 1 | 0.002 (0.001) | 1 | / | 1 |
| Radiance: Urban | / | / | 0.010 (0.007) | / | -0.025 (0.010)* | / | / | 0.77e-3 (0.30e-3)* | 0.029 (0.015). | / | / | / | / |
| Radiance: Wetland Length variables | / | -0.683 (0.492) | 0.016 (0.006)** | -0.153 (0.083). | / | / | 0.012 (0.007) | 0.12e-3 (0.22e-3) | 1 | -0.001 (0.001) | -0.002 (0.002) | -0.011 (0.032) | / |
| Hedgerow | / | / | -0.020 (0.008)* | 0.053 (0.068) | / | / | / | / | 1 | 0.002 (0.001) | / | -0.051 (0.040) | / |
| Road | / | / | / | / | -0.031 (0.008)*** | 0.003 (0.003) | / | 0.001 (0.30e- 3)*** | 0.007 (0.010) | 0.001 (0.001) | / | / | -2.865 (0.950)** |
| Road ² | / | / | / | / | 1 | 1 | / | -0.001 (0.30e-3)*** | 1 | / | / | / | 1 |
| Wooded edges | / | 0.101 (0.463) | / | 0.084 (0.060) | 0.023 (0.008) ** | 0.004 (0.003) | -0.007 (0.008) | 0.001 (0.30e- 3)*** | 1 | / | 0.006 (0.002)** | -0.049 (0.038) | / |
| Radiance: Hedgerow | / | / | 0.012 (0.007). | / | / | / | / | / | / | -0.001 (0.001) | / | / | / |
| Radiance: Wooded edges | / | -0.917 (0.501). | 1 | / | / | -0.002 (0.003) | / | / | 1 | / | 0.001 (0.002) | 1 | / |

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Fig. 3. Relation between the predicted number of bat passes per night and radiance values predicted from best models for species or species groups significantly affected by the radiance variable alone (i.e. a global effect apart from its interactions with landscape variables), and associated 95% confidence intervals. Circles show each of the 253 recording sites.

mitigated the negative effects of streetlights on bats (Mathews et al., 2015; Pauwels et al., 2019). One proposed explanation for positive effects is that tree cover could reduce the predation risk linked to light and could also, combined with streetlights, attract more insects and therefore constitute advantageous foraging grounds. Alternatively, close to trees, flying bats could also benefit from favourable microclimate or more structured flightpaths, which offset lighting-generated disadvantages. In our study, we found such mitigating of radiance effects only from increasing proportion of farmland areas and from decreasing distance to wetlands, for *N. noctula*, and *M. schreibersii*, respectively.

For species found to be negatively impacted by radiance in our study, we found P. pipistrellus to be more impacted at sites with highest length of hedgerows and closest to wetlands, and Myotis spp. to be more impacted at highest distances to urban. As hedgerows constitute a key landscape element for bat commuting (Pinaud et al., 2018), lighting at such linear landscape elements may disconnect foraging habitat and even limit their accessibility for bats (Laforge et al., 2019). In addition, we should be cautious about results for P. pipistrellus and confirm them in further studies, given that these were only significant at the most restrictive threshold of maximum error rate tolerance (MERT) in acoustic data (Barré et al., 2019). Wetlands also play an important role for foraging and for drinking for most bat species (De Conno et al., 2018; Roeleke et al., 2016), and light sources close to wetlands particularly attract aquatic insects (Manfrin et al., 2017) and in turn potentially induce an insects depletion around due to the "vacuum cleaner" effect. Thus, negative effects of ALAN on slow-flying gleaner species would be stronger close to wetlands. Finally, given that an increasing proportion

of urban areas reduce the amount and complexity of available vegetation and in turn of arthropod food resource (Sánchez-Bayo & Wyckhuys, 2019), and since insectivorous bat species strongly depend of high levels of vegetation complexity (Suarez-Rubio et al., 2018) and arthropods amounts (Charbonnier et al., 2014), it is not surprising to find mainly higher negative impacts of radiance in non-urban habitats. Laforge et al. (2019) draw similar conclusions showing that lighting reduction was more efficient to restore bat presence in vegetated areas than in cities.

P. pygmaeus activity increase with illumination, especially on farmland. Despite a sampling design elaborated for minimising correlations between land-use variables, we observed an opposition between urban and farmland cover in our study sites (correlation coefficient: 0.59; Table S8). Thus, found effects of radiance according to the farmland variable could mirror that non-urbanized areas are more attractive than urbanized areas (Border et al., 2017). Further studies remain needed to investigate why P. pygmaeus is especially active in lit more than dark farmland. H. savii and P. nathusii were also found to be more affected at sites with high forest proportions. Forest edges can drive activity and foraging of P. nathusii more than other habitats as hedgerows (Heim et al., 2017), while, to our knowledge, no similar studies have tested the same for H. savii. We hypothesize that the interest of forest edges coupled with lighting attracting arthropod prey (Owens & Lewis, 2018) could enhance the attractiveness of such habitat for these species. We also found M. schreibersii to be more affected by radiance at the lowest urbanized sites, and P. kuhlii to be increasingly affected with increasing distance to urban. Such a result is also consistent with the hypothesis we discussed above for aerial-hawking flying species: increasing amount of



Fig. 4. Predicted number of bat passes from GLMMs according to the interaction between radiance and land-use variables computed as (A) proportions and (B) distances. The colour scale represents the predicted mean number of bat passes per night, darker colours show higher number of bat passes. Circles represent each of the 253 combinations between radiance and land-use values sampled in the study. Predictions were restricted to the maximum convex polygon of sampled radiance-landscape variables combinations, and white surfaces show uncovered gradients. For each plot, the bat guild (i.e. aerial-hawing or slow-flying gleaner species) and the direction of bat response to radiance are shown with acronyms and symbols. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)



Fig. 5. Predicted number of aerial-hawking species passes from GLMMs according to the radiance in interaction with (A) the length of hedgerows in a 800 m radius for *P. pipistrellus* and (B) the distance to hedgerow for *N. leisleri*. The colour scale represents the predicted mean number of bat passes per night, darker colours show higher number of bat passes. Circles represent each of the 253 combinations between radiance and land-use values sampled in the study. Predictions were restricted to the maximum convex polygon of sampled radiance-landscape variables combinations, and white surfaces show uncovered gradients. Both plots show a negative effect of light on bat taxa. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

urban areas leads to a decreasing amount of other land-uses, which in turn reduces arthropod prey availability for bats, artificial light attractivity being therefore less efficient in such a landscape.

4.3. Limitations and perspectives

Most effects found were robust against error rates in acoustic data and the presented interactions did not suffer from any confounding effects between radiance and land-use variables. However, results validity could not be checked at the 0.2 MERT threshold for *E. serotinus*, *N. noctula* and *P. nathusii*, potentially because of too low remaining numbers of bat passes, given that such thresholds discarded a lot of data (Table S11; Supporting information S5).

Satellite-based data used in this study were calculated using cloudfree images, which potentially underestimate impacts for weather conditions promoting a skyglow caused by upwardly emitted artificial light being scattered in the atmosphere (Kyba et al., 2015). Our bat monitoring was carried out under non-negligible cloud covers which varied from 17 to 70% (47% in average; Table S2) over the 27 nights studied, which could significantly increase skyglow. Since a skyglow can be comparable to late twilight and moonlight (Gaston et al., 2017), we could expect it to affect the use of space by bats (Roeleke et al., 2018) and in turn the ALAN effects-landscape relationship. Further studies could thus assess how the skyglow, and more generally less favourable weather conditions, would impact results we report in this study. In addition, further studies should compare such results from the VIIRS raster with ones from more local light intensity measurements to study finer-scale factors, as performed in Straka et al. (2019), Pauwels et al. (2019) and Hale et al. (2015). Indeed, given that our explanatory variable was a radiance pixels averaging in a given radius around sites, there is undeniably an inaccuracy in the real distances of impact. Accurate distances of impact are nevertheless essential for concrete recommendations in local lighting management. In addition, although land-uses used in this study to describe landscape composition were the most accurate information we had, future studies could assess ALAN effects on bats according to landscape composition using (i) more accurate spatial resolution of ALAN data and (ii) finer habitat descriptors, for example by differentiating different types of farming in the farmland category, or by measuring structure of woody habitats.

Although we found some positive effects of radiance, artificial lighting is expected to induce negative effects on a larger scale (Azam et al., 2016), likely due to prey accumulation and 'vacuum cleaner effect' around light sources decreasing prey availability on larger scales (Eisenbeis, 2006; Owens and Lewis, 2018). As a consequence, positive relationships at local scale between bat activity and ALAN should be interpreted with caution. Finally, one group (*Plecotus* spp.) remains strongly negatively affected by ALAN effects irrespective of landscape composition, which in turn involves thinking of reduction possibilities everywhere for this group.

5. Conclusions

Artificial light effects on bats were predicted to vary according to landscape composition, but had so far not received attention at a regional scale for a large number of landscape predictors and bat taxa. We show that the magnitude of most ALAN effects on bats is driven by landscape composition. Some ALAN effects were even only detectable in particular landscape compositions, making the main effect of ALAN undetectable without account for interactions with landscape. This underpins the great importance to prioritize ALAN reduction schemes for bat conservation in non-urban habitats, and how important is to account for landscape composition when studying ALAN effects on bats to avoid missing effects. Indeed, most found effects occurred in non-urban habitats, thereby highlighting the importance of minimising lighting close to these areas.

Author statement

KB conceived the ideas; KB, AV, AD and SV designed the methodology; AD and AV collected the data; AD, AV and TD manually checked bat passes; KB and AV analysed the data; KB with the support of CK, CA, AV and IL led writing of the manuscript. All authors critically contributed to the drafts and gave their final approval for publication.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.envpol.2021.118394.

Data accessibility

Dataset used are available at https://doi.org/10.5281/zenodo. 5585373.

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